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BOTANICAL GAZETTE

FEBRUARY, 1901

THE PHYSIOGRAPHIC ECOLOGY OF CHICAGO AND VICINITY; A STUDY OF THE ORIGIN, DEVELOPMENT, AND CLASSIFICATION OF PLANT SOCIETIES.

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY.
XXIV.

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(WITH THIRTY-FIVE FIGURES.)

I. The content and scope of physiographic ecology.

WITHIN the last few years the subject of ecology has come to find a place of more or less importance wherever botany is studied in its general aspects. The limits of the subject, however, have not yet been defined, nor have many attempts been made to bring order out of the chaos which exists with regard to the arrangement of the subject-matter. The main purpose of the present paper is to suggest a classification of a portion of the ecological field.

Whatever its limits may be, ecology is essentially a study of origins and life histories, having two well-marked phases; one phase is concerned with the origin and development of plant structures, the other with the origin and development of plant societies or formations. The plant structure side again has two aspects, one viewing organs or plant forms as a whole, the other viewing the tissues which make up the organs; the former might

be called organographic ecology or even organography, while the latter may be called ecological anatomy.

It may be well to speak more in detail concerning the distributional phase of ecology. There are two distinct aspects here also, the one local, the other regional. Climatic factors, particularly temperature and atmospheric moisture, permit the subdivision of the earth into great zones or regions with characteristic plant formations which extend over wide areas. Examples of this type are tropical evergreen forests, deserts in continental interiors, prairies, deciduous forests, arctic tundras. These formations are widespread because the factors that produce them are widespread. We might call these formations climatic formations (following Schimper¹) and the subject that deals with them geographic ecology or ecological plant geography. In contrast with the above there are the local or edaphic factors, such as soil (including its moisture, air, and temperature relations), slope, light; in other words, factors that are largely due to the physiographic nature of the district. Where the climate is the same these factors produce marked changes locally, and there results a variety of plant societies, such as swamp, dune, bottom forest, river bluff, etc. These correspond to Schimper's¹ edaphic formations or Warming's plant societies, and the subject that deals with them may be called physiographic ecology.

In order to justify the terminology here given it will be desirable to trace briefly the history of the study of plant societies and then to depict the intimate relations which exist between the physiography of a region and its flora. Before the appearance of Warming's ecological plant geography² there had been no attempt to classify the plant formations of the globe in a systematic manner. Warming introduced the term plant society in place of plant formation, because of the varied use of the latter,

¹SCHIMPER, A. F. W.: *Pflanzengeographie auf physiologischer Grundlage* 173-176. Jena, 1898.

²WARMING, E.: *Plantesamfund*. Copenhagen, 1895. German edition, translated by Knoblauch. Berlin, 1896.

and made variations in the water content of the soil a basis of classification. Plant societies were divided into hydrophytes, mesophytes, and xerophytes; further than this, however, little attempt was made by Warming to subdivide the plant societies, except in the case of swamp and dune plants. In these two instances, as will appear later, Warming adopted the order of succession in his method of treatment.

Since Warming's great work appeared, ecologists have in general followed his ideas and have attempted to work them out. Noteworthy contributions have also been made which make a comprehensive view of the subject more possible. Schimper³ has analyzed in a most thorough manner the conditions which determine the distribution of plants in the large, though he has discussed but briefly the purely local or habitat factors. We owe to him, however, the first clear statement of the distinction between edaphic and climatic factors and formations. The minuter treatment of the edaphic formations did not lie within his field, and he has attempted in no sense to give a classification, except in the case of climatic formations.

Graebner^{4,5} has published a classification of some of the German vegetation formations, which has not received the attention it deserves. This classification is based in the main on the chemical and physical characteristics of the soil. The primary divisions are chemical, depending on the richness or poverty of the soil in plant foods. The secondary divisions are based chiefly on soil moisture.

N. H. Nilsson⁶ in some preliminary notes on Swedish swamps and their vegetation called attention to the striking difference between hydrophytic and xerophytic swamps, and

³ *Op. cit.*

⁴ GRAEBNER, P.: Gliederung der westpreussischen Vegetationsformationen. Schrift. Naturf. Ges. Danzig 9: 43-74. 1898. See Bot. Centralb. 75: 277-279. 1898.

⁵ GRAEBNER, P.: Ueber die Bildung natürlichen Vegetationsformationen im norddeutschen Flachlande. Archiv der Brandenburgia 4: 137-161. 1898. See Bot. Centralb. 77: 212-214. 1899.

⁶ NILSSON N. H.: Einiges über die Biologie der schwedischen Sumpfpflanzen. Bot. Centralb. 76: 9-14. 1898.

gave expression to the view that differences in food supply may account for the facts observed. Schimper⁷ has a somewhat similar view, but explains differences in the vegetation of various swamps more along the line of relative ease or difficulty of absorption in the swampy soils. Both Nilsson and Schimper regard peat bogs as essentially xerophytic.

In this historical sketch mention should be made of the work of Flahault^{8,9}, who has projected and begun to execute a detailed map of the plant societies of France. Conventional color tones are chosen for the various plant societies, and they are plotted on topographic contour maps. Robert Smith^{10, 11} had just entered upon a similar work in Scotland when death put a stop to his labors. So far as the author knows, Flahault has not concerned himself particularly as yet with the matter of classification. Alb. Nilsson¹² has recently published some interesting studies of Swedish plant societies, tracing the order of succession of vegetation on cliffs and moors. Still more recently Meigen¹³ has published a series of short articles, tracing the order of succession in a number of plant societies. Besides the authors named thus far, Drude¹⁴, MacMillan¹⁵, and Pound and Clements¹⁶ have given excellent treatments of the plant formations in their respective regions.

⁷ *Op. cit.* 18.

⁸ FLAHAULT, Ch.: *Projet de carte botanique forestière et agricole de la France*. Bull. Soc. Bot. France 41:56-94. 1894. Ann. de Géographie 5:449-457. 1896.

⁹ FLAHAULT, Ch.: *Essai d'une carte botanique et forestière de la France*. Ann. de Géographie 6:289-312. 1897, etc.

¹⁰ SMITH, ROBERT: On the study of plant associations. Nat. Sci. 14:109-120. 1899.

¹¹ SMITH, ROBERT: Botanical survey of Scotland. I. Edinburgh district. II. North Perthshire district. Scot. Geog. Mag. 16:385-416; 441-467. 1900.

¹² NILSSON, ALB.: Några drag ur de svenska växtsamhällellenas utvecklingshistoria. Bot. Not. 1899:89-101; 123-135.

¹³ MEIGEN, FR.: Beobachtungen über Formationsfolge im Kaiserstuhl. Deutsch. Bot. Monatsschrift 18:145-147, etc. 1900.

¹⁴ DRUDE, O.: Deutschlands Pflanzengeographie, I. Teil. Stuttgart. 1896.

¹⁵ MACMILLAN, C.: Observations on the distribution of plants along shore at Lake of the Woods. Minn. Bot. Stud. 1:949-1023. 1897.

¹⁶ POUND and CLEMENTS: The phytogeography of Nebraska. I. General Survey. Lincoln. 1898.

During 1896 and 1897 the author of this paper, in company with his students, endeavored to classify the vegetation about Chicago in accord with Warming's principles. In 1898 a similar and more careful study of this kind was made in northern Michigan. It was of course found to be possible to classify the plant societies by the amount of water in the soil, but it was found that such a classification put together plant societies radically different in their character, and separated plant societies that were obviously closely related. The best instances of these difficulties were seen in the case of heaths and moors. Not only were heaths and moors found to have closely similar species and vegetative adaptations, but these plant societies were often found grading into each other. In water content these societies were very different, the peat moor or bog being hydrophytic and the heath xerophytic. Thus some factor other than water content is responsible for both. In that same year (1898) Nilsson and Schimper published their views on the causes of the xerophytic character of moor vegetation, as outlined above. Furthermore the vegetation of peat bogs is radically different from that of river swamps which have the same water content.

Further field study but added to the difficulties of the situation, and the need of another classification was keenly felt. It was seen at once that no one factor could take the place of the water content of the soil, since that is obviously the most important of all direct factors in distribution, as Warming so ably shows. An attempt was therefore made to relate the facts of distribution to combinations of factors, with the following results. The classification which is about to follow is based in the main on two ideas, viz., that a classification to be true must be genetic and dynamic. In other words, an attempt is made to group plant societies according to their relationship and their evolution.

The influences which govern the distribution of plants reside in the air or soil (regarding water as soil, for the sake of convenience). The atmospheric influences (light, heat, air) operate over wide areas and have subordinate edaphic importance,

whereas the soil influences (soil heat, soil air, soil water, soil chemistry and physics) are of predominant edaphic importance, though of little account when distribution over wide areas is considered. We may say then that atmospheric or climatic factors determine distribution in the large, while local differences are produced by changes in the edaphic or soil factors.

The soil conditions are chiefly determined by the surface geology and the topography. The original character of the soil, whether rock, sand, clay, or marl, depends upon the geological relations. From the vegetation standpoint the topographic relations are commonly much more important, since they condition the presence or absence of drainage, and hence cause striking variations in air content and humus. Doubtless the characteristic features of peat bog vegetation are due to the absence of drainage and consequent poor aeration and accumulation of organic products. Moreover, in so far as the atmospheric factors have an influence on distribution locally, it is largely due to topographic diversities, such as angle and direction of slope.

Having related the vegetation largely to topography, we must recognize that topography changes, not in a haphazard manner, but according to well-defined laws. The processes of erosion ultimately cause the wearing down of the hills and the filling up of the hollows. These two processes, denudation and deposition, working in harmony produce planation; the inequalities are brought down to a base level. The chief agent in all these activities is water, and no fact is better established than the gradual eating back of the rivers into the land and the wearing away of coast lines; the material thus gathered fills up lakes, forms the alluvium of flood plains, or is taken to the sea. Vegetation plays a part in all these processes, the peat deposits adding greatly to the rapidity with which lakes and swamps are filled, while the plant covering of the hills, on the contrary, greatly retards the erosive processes. Thus the hollows are filled more rapidly than the hills are worn away. As a consequence of all these changes, the slopes and soils must change;

so, too, the plant societies, which are replaced in turn by others that are adapted to the new conditions.

There must be, then, an order of succession of plant societies, just as there is an order of succession of topographic forms in the changing landscape. As the years pass by, one plant society must necessarily be supplanted by another, though the one passes into the other by imperceptible gradations. Here then is a classification both genetic and dynamic, a classification which has a place for all possible ecological factors. It is based on the normal physiographic changes of a region and hence should be called a physiographic classification. One thing more must be recognized, and that is that environmental influences are normally cumulative. A plant society is not a product of present conditions alone, but the past is involved as well. For example, a hydrophytic plant society may be seen growing in a mesophytic soil; the author has seen a mesophytic tamarack swamp which can be explained only in this way. We have in this phenomenon a lagging of effects behind their cumulative causes, just as the climax of the heat in summer comes long after the solstice.

In a classification like this great emphasis is placed on border lines or zones of tension, for here, rather than at the center of the society, one can best interpret the changes that are taking place. Of course the order of succession referred to above is a vertical or historical one. One plant society is said to follow another if it is actually superimposed upon the one preceding. In many cases, if not in most, there is a horizontal order of succession at the present time that resembles the vertical succession of which we now have only the topmost member. Instances of similarity between vertical and horizontal orders of succession are well shown in peat swamps and along shores and flood plains. Along a sandy shore it is only by studying the horizontal succession that one can get any idea of the vertical, since all fossil traces of preceding plant societies have passed away. In peat swamps one can sometimes verify the results of a horizontal zonal study by investigating the fossil remains beneath

We may now outline the main features of a physiographic classification of plant societies. Speaking in the large, the tendency of the erosive processes is to reduce the inequalities of the topography and produce a base level. This base level may not soon be reached, though geological history furnishes instances of extensive base leveling. Crustal movements interfere with the erosive agencies and a mature base level topography may become rejuvenated by a great uplift of the land, or sinking on the other hand may check the rapid action of erosion. Yet even with the crustal movements there go these topographic changes and with them the plant societies must change. Putting the facts of physiography in the terms of ecology, the conditions become more and more mesophytic as the centuries pass. In a young topography, such as the recently glaciated areas of Michigan, Wisconsin, and Minnesota, there is a great variety of topographic conditions and of plant societies. Among these are many hydrophytic lakes and swamps and many xerophytic hills. The hills are being denuded and the swamps and lakes are being filled, so that the hydrophytic and xerophytic areas are becoming more and more restricted, while the mesophytic areas are becoming more and more enlarged. In passing from youth to old age then, a region gradually loses its hydrophytic areas and also its xerophytic areas, though in the latter case there is usually at first an increase in the xerophytic areas which is due to the working back of the young streams into the hills. The latter conditions are well shown in Iowa; in the comparatively recent Wisconsin drift of north-central Iowa the topography is much less diversified and there are fewer xerophytic areas than in the older Iowan drift farther south, which has been greatly dissected by stream erosion. Later, however, the inequalities are removed, and we find great mesophytic flood plain areas, such as are seen along the lower Mississippi.

From what has been stated it will be seen that the ultimate stage of a region is mesophytic. The various plant societies pass in a series of successive types from their original condition to the mesophytic forest, which may be regarded as the climax

or culminating type. These stages may be slow or rapid; some habitats may be mesophytic from the start; undrained lakes and swamps fill up and become mesophytic with great rapidity, whereas granite hills might take many centuries or even geological epochs in being reduced to the mesophytic level. Again the stages may be direct or tortuous; we have already seen how the first consequences of stream erosion may be to make mesophytic areas xerophytic. So, too, in flood plains, the meanderings of the river may cause retrogressions to the hydrophytic condition such as are seen in oxbow lakes, or the river may lower its bed and the mesophytic flood plain become a xerophytic terrace. But through all these changes and counterchanges the great mesophytic tendency is clearly seen; mesophytic areas may be lost here and there but many more are gained, so that the approach to the mesophytic base level is unmistakable. Moreover, the retrogressive phases are relatively ephemeral, while the progressive phases often take long periods of time for their full development, especially in their later stages.

The above phenomena postulate congenial climates and more or less static crustal conditions. It is obvious, however, that erosive processes in a desert region do not result in a mesophytic flora; the same is true of alpine and arctic climates. Again, the climate of all regions is doubtless changing, as it has changed in past ages. So, too, there are crustal movements up and down. In other words the condition of equilibrium is never reached, and when we say that there is an approach to the mesophytic forest, we speak only roughly and approximately. As a matter of fact we have a variable approaching a variable rather than a constant. These conditions do not destroy the validity of a physiographic classification, but rather they require an enlargement of conception. Retrogressive phases, *i. e.*, away from the mesophytic and toward the hydrophytic or xerophytic, must be included, as well as progressive phases away from the hydrophytic or xerophytic and toward the mesophytic. In this way all possible conditions are accounted for. For example, upward crustal movements make hills more xerophytic and swamps more

mesophytic, whereas downward movements make hills more mesophytic and swamps more hydrophytic. Thus in the upward movement of hills and the downward movement of swamps, physiographic processes are more or less neutralized and we may speak of retrogressive tendencies ; in the other two cases physiographic processes are accelerated and we have more rapid progress toward the mesophytic climax. If a climate grows colder or more arid, we find retrogressive tendencies toward the xerophytic condition, while in a climate that is getting more moist or more genial the mesophytic tendencies of the erosive processes are accelerated. Furthermore, climatic and crustal changes are commonly so slow in comparison with physiographic changes, that it is usually difficult to decipher their tendencies. We can be far more sure, in other words, with relation to the past and future of a topographic form and its plant societies, so far as erosion is concerned, than we can as to the actual effect that changing climatic and crustal conditions are making.

One other modification of the physiographic theory is necessary, as has been clearly shown by recent field studies. While changes in plant societies are certain to follow changes in topography, it does not necessarily follow that plant societies remain the same if topographic conditions remain unchanged. In other words, changes may take place in plant societies more rapidly than in the topography. A cycle of vegetation may be much shorter than a cycle of erosion. One of the most interesting cases of this is seen in a growing river system. In the ravine stage there may be a rapid change from the xerophytic to the mesophytic plant societies on the slopes. As the valley widens xerophytic conditions appear on the slopes once more. This first and relatively short-lived mesophytic condition may be called a temporary climax, in distinction to the more permanent climax of the base level.

In a study of plant societies such as this, it must be recognized that orders of succession are not the same in various regions. There is probably a close analogy between the various society life histories where climatic conditions are the same, but

it remains true, nevertheless, that each region must be worked out by itself. The general principles that are involved in the dynamics of plant societies, however, ought to be essentially the same everywhere. Some instances will be given which will show the necessity for working out the life history of the plant societies in all regions. While the culminating type throughout the northern states east of the Mississippi river is probably a deciduous mesophytic forest, yet the elements of this forest differ greatly in different localities. In central Michigan the maple, beech, and the evergreen hemlock appear to be the leading character trees of the mesophytic forest. In Indiana and Illinois the hemlock is not one of the dominant trees of this forest. In the Alleghanies of Tennessee a large number of tree species assume a place of almost equal importance in the mesophytic forest. Again, in the Chicago region the tulip tree and buckeye are rare and confined to the flood plain forests, while in Tennessee these trees are found in many other plant societies. In the Chicago region the arbor vitae is confined to undrained swamps and xerophytic cliffs, while in northern Michigan it is found in many other habitats. We may perhaps summarize these data by saying that each species varies in habitat in different regions, and that in general a species can grow in the largest number of plant societies at its center of distribution, since there the climatic conditions favor it most highly. In other regions, especially near its areal limits, it can grow only in those plant societies which resemble most closely in an edaphic way the climatic features at the distribution center. Thus the tulip and buckeye, which flourish best in the mesophytic forest climate of the Alleghanies, are found near Chicago only in the most pronounced of our mesophytic societies, those of the flood plain. Again, the arbor vitae, and with it many conifers and heaths, grow near Chicago only on the cliffs and dunes or in the undrained swamps, since these are the most pronounced of our xerophytic habitats and most closely resemble the xerophytic northern climates.

A few words should be said in the way of indicating the

relationship between this and other classifications. Warming's classification, based on the water relations, at two points agrees with the physiographic theory, viz., in the treatment of swamps and dunes. Each of these is treated from the standpoint of the order of succession as revealed by zonal distribution, though in the case of the dunes this order is not one of decreasing or increasing water content. Alb. Nilsson and Meigen (see above), and for that matter many other authors, have studied various plant societies from the standpoint of their order of succession, but so far as the author is aware no previous attempt has been made to establish a comprehensive theory on this basis. Graebner's classification (see above) has several points in common with the physiographic theory, especially as it relates heaths with moors. In this connection it will be of interest to refer to a paper by J. B. Woodworth¹⁷ which indicates a fertile line of research that is but now being taken up by biologists. He shows how the base-leveling processes must influence the evolution of species, since these processes constantly erect new and destroy old barriers, and hence cause isolation in the one case and intermingling of species in the other. Woodworth gives a number of instances of the influence of base leveling upon animal life, and he refers, although but slightly, to the changes which must take place in the plant life as regions are uplifted or approach base level. It seems surprising that such a great field of study has been neglected until now. C. C. Adams, in a paper as yet unpublished, and C. T. Simpson¹⁸ have recently given special cases of the interrelations between physiographic changes and animal distribution.

The general principles of the physiographic theory have been developed as a result of studies in various sections of the country. Since 1898, when the author first began to work along these physiographic lines, the main thought has been to subject

¹⁷ WOODWORTH, J. B.: The relation between base-leveling and organic evolution. *Am. Geol.* **14**: 209-235. 1894.

¹⁸ SIMPSON, C. T.: On the evidence of the Unionidae regarding the former course of the Tennessee and other Southern rivers. *Science N. S.* **12**: 133-136. 1900.

the theory to the most rigid test possible. In connection with a number of students, investigations have been carried on about Chicago, in northern Michigan, in Tennessee, and along the Atlantic coast. In all cases it has been possible to find a general consonance between the facts of distribution and the principles as stated above. The theory has suffered many modifications since its first conception, and doubtless it will suffer more. Indeed, it may be discarded altogether for some other better theory. Nevertheless, publication at this time seems to be justified, and it is hoped that this paper may aid in solving some of the riddles of ecology.

The author especially wishes to mention in this place the work of his student and associate, Mr. H. N. Whitford, who has in preparation a physiographic study of the forests of northern Michigan. The author is likewise especially indebted to another of his students, Mr. W. B. McCallum, who has taken all of the photographs with which this paper is illustrated, with the exception of *figs. 7 and 13*, which were contributed by Professor J. J. Allison, of Joliet. Acknowledgment should also be made of the help given by three excellent papers which deal with the general physiographic and geographic features of the Chicago area. To these works by Leverett,¹⁹ Blatchley,²⁰ and Salisbury and Alden²¹ the author has made constant reference. The author has likewise freely used the work of Higley and Raddin.²²

In the following pages the various series of the Chicago area are discussed in some detail. Two general groups are made, the inland and the coastal. The inland group is subdivided into three series, river, swamp, and upland. The coastal group is subdivided into two series, lake bluff and dune. The river series

¹⁹ LEVERETT, F.: The Pleistocene features and deposits of the Chicago area. Chicago, 1897.

²⁰ BLATCHLEY, W. S.: The geology of Lake and Porter counties, Indiana. Reprint from the Twenty-second Annual Report of the Department of Geology and Natural Resources of Indiana. Indianapolis, 1897.

²¹ SALISBURY, R. D., and ALDEN, W. C.: The geography of Chicago and its environs. Chicago, 1899.

²² HIGLEY, W. K., and RADDIN, C. S.: The flora of Cook county, Illinois, and a part of Lake county, Indiana. Chicago, 1891.

is remarkably tortuous, involving constructive and destructive, progressive and retrogressive phases. The treatment begins with an erosion gully; then there follow in order the ravine, both in clay and in rock, the xerophytic bluff, and the mesophytic forest. The depositional phases of the river begin with the appearance of a permanent stream; then follow the various stages of the flood plain culminating in the mesophytic forest. The swamp series begins with the pond, treats next the various types of swamps and ends with a brief discussion of the prairie. In the upland series the various stages of the rock hills and then of the clay hills are taken up in turn, culminating in the mesophytic forest. The coastal group is next discussed, beginning with the lake bluff. Finally, there is a brief treatment of the dune series from the beach on through the embryonic and active dune to the established dune on which there finally appears the mesophytic forest.

II. The plant societies.

A. The inland group.

I. THE RIVER SERIES.

A. *The ravine*.—No topographic forms lend themselves so well to a physiographic sketch of the vegetation as do those that are connected with the life history of a river. Beginning with the ravines, which are deep and narrow, because of the dominance of vertical cutting, we pass to the broader valleys, where lateral cutting becomes more pronounced. From this stage on we have to deal with two phases of river action, the destructive, which is concerned with the life history of the bluff, and the constructive, which has to do with the development of the flood plain.

Wherever there is an elevated stretch of land adjoining a body of water, such as a lake bluff, one is apt to find excellent illustrations of the beginning of a ravine. *Fig. 1* shows an embryonic ravine of a type that may be seen frequently along the clay bluffs between Evanston and Waukegan. A ravine of this type is essentially a desert, so far as plant life is concerned.

The exposure to wind and to alternations of temperature and moisture is excessive. The lack of vegetation, however, is due chiefly to the instability of the soil; this instability is particularly great in the case of clay bluffs such as these, where the seepage of water causes extensive landslide action. No plants can get a foothold in such a place, unless it be a few species that may be able to make their appearance between periods of landslide action; among these plants annuals particularly predominate. The perennials that may be found in such places are almost entirely plants which have slid down the bank. Near the center of *fig. 1* is a clump of shrubs that has slid down in this way. Ravines of a similar type may also be seen at many places inland, and wherever found the poverty of vegetation on the slopes is the most striking character.

As a ravine extends itself inland the conditions outlined above may be always seen about its head, but toward the mouth of the ravine the slopes are less precipitous. Torrents cut down the bed of the ravine until a depth is reached approaching the water level at its mouth. From this time on the slopes become reduced and the ravine widens more than it deepens, by reason of lateral cutting, landslide action, and side gullies. After a time a sufficient stability is reached to permit a considerable growth of vegetation. If the erosion is slight enough to allow a vegetation carpet to develop, a high degree of luxuriance may be attained. In fact ravine conditions are usually extremely favorable for plants, after the initial stages have passed. In a comparatively few years the vegetation leaps as it were by bounds through the herbaceous and shrubby stages into a mesophytic forest, and that, too, a maple forest, the highest type found in our region. Nothing shows so well as this the brief period necessary for a vegetation cycle in a favored situation when compared with an erosion cycle.

Of such interest are the facts just noted that it is worth while to mention some of the characteristic ravine plants. Perhaps the most characteristic trees of the Glencoe ravines are the basswood (*Tilia Americana*) and the sugar maple (*Acer saccharinum*),

though the ash, elm, and other trees are frequent. The most characteristic undershrub is the witch hazel (*Hamamelis Virginiana*). The herbaceous plants are notoriously vernal forms, such as *Hepatica*, *Thalictrum*, *Trillium*, *Mitella*, *Dicentra*, *Sanguinaria*; mosses abound and liverworts are frequent. A ravine with the above vegetation is shown in *fig. 2*. We can explain this flora only by regarding it as having reached a temporary climax. Ravine conditions are more favorable for plants than those that precede or follow. The instability and exposure of the gully have gone; in their place there is protection from wind and exposure. The shade and topography favor the collection and conservation of moisture, and as a result there is a rapid development into a high-grade forest, as outlined above.

Rock ravines are much less common in the Chicago area than are those of clay, since the underlying limestone rarely comes near the surface. Excellent illustrations of stream gorges are to be seen at Lockport, and also in various tributaries of the Illinois river near Starved rock. A striking difference between these rock gorges or cañons and the clay ravines is in the slope of the sides. The physical nature of the rock excludes landslide action, hence the sides are often nearly vertical for a long time. Lateral cutting is also relatively slow as compared with clay. Thus the conditions for vegetation at the outset are much more favorable than in a clay ravine. Rock-bound gorges are very shady and often dripping with moisture, hence liverworts and many mosses find here a habitat even more congenial than in the clay. Among the higher forms are found the most extreme shade plants that we have, such as *Impatiens*, *Pilea*, and shade-loving ferns, plants whose leaves are broad and remarkably thin. *Figs. 3* and *4* represent cañons of the above description, whose rocks drip with moisture.

The stages of development pass much more slowly in cañons than in clay ravines, largely because the primitive conditions of shade and moisture remain for a long period of time. Nor do the steep slopes permit the development of a wealth of trees and shrubs, since a secure foothold is not easily found. However,

as the cañon broadens out and the slopes become less steep, shrubs and trees come in, though a typical mesophytic forest is rarely seen. The Starved rock ravines are cut in St. Peters sandstone, those at Lockport in the Niagara limestone, yet the vegetation in the two places is essentially alike; at any rate the resemblances are greater than the differences. Much has been



FIG. 1.—Embryonic ravine in the lake bluff at Glencoe. Entire absence of vegetation on the unstable clay slopes with the exception of shrubs and grasses that have slid down from the top.

written on the physical and chemical influences of rocks upon the vegetation. The facts seen here seem to show that the physiographic stage of a region is more important than either. The flora of a youthful topography in limestone, so far as the author has observed, more closely resembles the flora of a similar stage in sandstone than a young limestone topography resembles an old limestone topography. A limestone ravine resembles a sandstone ravine far more than a limestone ravine resembles an exposed limestone bluff or a sandstone ravine resembles an

exposed sandstone bluff. We may make the above statements in another form. Rock as such, or even the soil which comes from it, is of less importance in determining vegetation than are the aerial conditions, especially exposure. And it is the stage in the topography which determines the exposure.

All of the preceding statements as to topographic stages,



FIG. 2.—Ravine at Glencoe with a mesophytic forest vegetation on the slopes (temporary climax). Presence of erosive forces indicated by leaning trees. Water in the stream bed only after rains.

whether young or old, refer not to times but to constructional forms. Two ravines, equally youthful from the topographic standpoint, may differ widely as to actual age in years or centuries, since erosion is more rapid in one rock than in another. In our region, however, elements of actual time are not very important, except as between rock and clay, since the limestone is less soluble and the sandstone is more easily eroded than is often the case.

B. *The river bluff*.—As a valley deepens and widens, the

conditions outlined above undergo radical changes. From this point it will be necessary to discuss two phases in the growing river, the bluff phase and the bottom phase. We have left the clay ravine bluffs in a state of temporary climax, clothed with luxuriant mesophytic forest trees and with a rich undergrowth of vernal herbs. More and more the erosive processes are conspicuous laterally, and widening processes prevail over the more primitive deepening. As a result, the exposure to wind, sunlight, and changes of temperature increases; the moisture content of the slopes becomes less and less. The rich mesophytic herbs, including the liverworts and mosses, dry up and die. The humus oxidizes more rapidly, and a xerophytic undergrowth comes in. In place of *Hepatica* and its associates, we find *Antennaria*, *Poa compressa*, *Equisetum hyemale*, and other xerophytic herbs; *Polytrichum* also replaces the mesophytic mosses. The first signs of the new xerophytic flora

are seen at the top of the ravine slope; indeed the original xerophytic plants may never have been displaced here by the ravine mesophytes. As the ravine widens, the xerophytic plants creep down the slope, often almost to the water's edge. Some of the young ravines between Evanston and Waukegan show xerophytes at the summits of the slopes. *Fig. 5* shows a

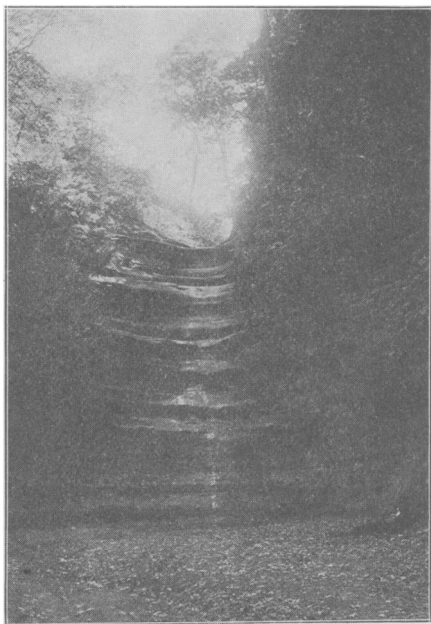


FIG. 3.—Head of a cañon in the St. Peters sandstone at Starved rock. Erosive forces prominent, and vegetation slight on the dripping slopes.

widening ravine at Beverly hills; the vegetation is much less luxuriant than that shown in the young ravine of *fig. 2*.

After a few years have passed, xerophytic shrubs appear on the bluff in place of the witch hazel and its associates. And it is not long until xerophytic or semi-xerophytic thickets prevail,

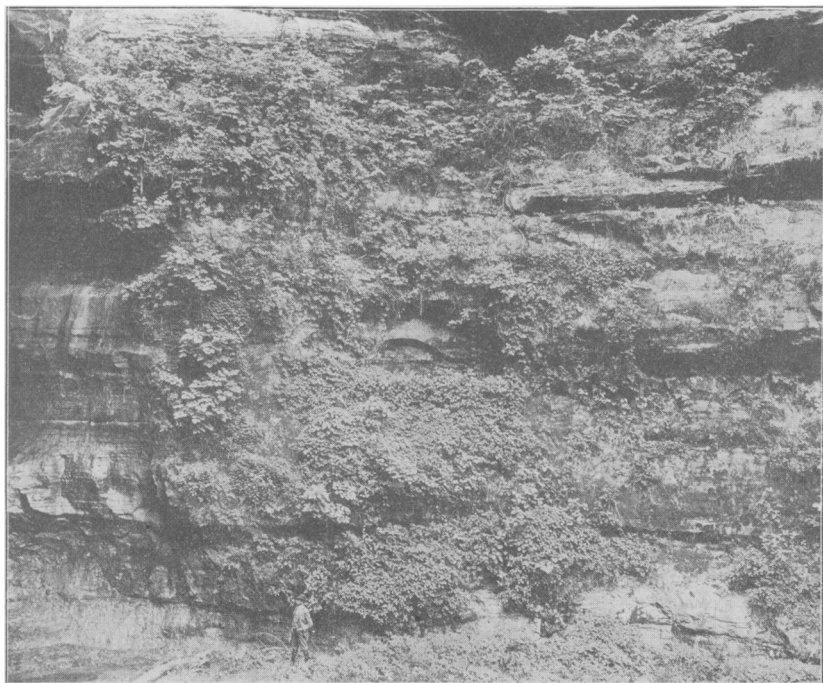


FIG. 4.—Side of a cañon in the St. Peters sandstone at Starved rock. Herbaceous shade vegetation on the precipitous slopes.

in place of the former mesophytic undershrubs. Among the more characteristic of these shrubs are the hop tree (*Ptelea trifoliata*), bittersweet (*Celastrus scandens*), sumachs (*Rhus typhina* and *R. glabra*), choke cherry (*Prunus Virginiana*), nine-bark (*Physocarpus opulifolius*), wild crab (*Pyrus coronaria*). Two small trees are common on stream bluffs, the service berry (*Amelanchier Canadensis*) and the hop hornbeam (*Ostrya Virginica*); this last species is perhaps the chief character tree of river

bluffs and is rarely absent. Perhaps the best examples of xerophytic stream bluffs near Chicago are along Thorn creek. One of the most interesting things about these bluff societies is the frequent presence of basswoods and sugar maples. Doubtless these trees look back to the mesophytic associations that have otherwise disappeared. As would be expected, the last of the



FIG. 5.—Open ravine at Beverly hills, showing gentle slopes covered with a less mesophytic vegetation than is shown in *fig. 2*. Dominance of oaks in place of maples and basswoods.

mesophytes to die are trees, because they are longer lived than herbs and shrubs, and also because their roots reach down to the moisture. But they cannot be succeeded by their own kind, inasmuch as the critical seedling stages cannot be passed successfully.

The life history of the rock ravines or cañons is somewhat different. When the ravine vegetation is at its height, the moisture and shade are greater here than in the clay, hence the high development of liverworts and their associates. As the ravine

widens these extreme shade forms are doubtless driven out almost immediately by xerophytes, since intermediate or mesophytic conditions are seldom seen where the soil is rock. Furthermore, the xerophytic conditions become much more extreme on rock bluffs than on clay bluffs. This is well illustrated at Starved rock (*fig. 6*), where the dominant tree vegetation is



FIG. 6.—Xerophytic bluff of St. Peters sandstone at Starved rock, on the Illinois river, showing conifers and other plants of dry rocks. Influence of erosive forces seen at the base.

coniferous, consisting especially of the white pine (*Pinus Strobus*) and the arbor vitae (*Thuja occidentalis*). The herbs and undershrubs here are also pronouncedly xerophilous, resembling the vegetation of the sand dunes, *e. g.*, *Selaginella rupestris*, *Campanula rotundifolia*, *Pellaea atropurpurea*, *Talinum teretifolium*, *Opuntia Rafinesquii*, etc. The entire bluff flora down to the river's edge is xerophytic, except in shaded situations.

When a stream in its meanderings ceases to erode at the base of a bluff, increased opportunity is given for plant life. Through

surface wash the slopes become more and more gentle. Mesophytic vegetation comes in at the foot of the bluff and creeps up as the slopes decrease. Finally the xerophytes are driven from their last stronghold, the top of the slope, and the mesophytes have come to stay, at least until the river returns and



FIG. 7.—Ravine in the Niagara limestone at Lockport, showing the beginnings of a flood plain.

ent rs upon another stage of cliff erosion. The growth of a ravine into a valley with xerophytic bluffs is rapid, when expressed in terms of geology, but far less rapid when expressed in terms of vegetation. A ravine in the vi or of youth may develop so slowly that forest trees may grow to a considerable size without any perceptible change in the erectness of their trunks. Thus in *figs. 2* and *5* it will be seen that most of the trees stand approximately vertical. But the activity of the erosive forces,

slow as it may be, is nevertheless revealed by occasional leaning or even falling trees. From the above it is easy to understand that cycles of vegetation often pass much more rapidly than cycles of erosion, but never more slowly. During one erosion cycle the mesophytic forest develops at least twice, once on the ravine slopes and then finally on the gentler slopes that betoken approach toward base level.



FIG. 8.—General view of the Illinois valley near Starved rock, showing islands and an extensive flood plain with trees along the margin. Young islands in the foreground, older islands in the background.

C. *The flood plain.*—We may now follow the successive stages in the development of the flood plain vegetation. While the ravine is still young, as in *fig. 2*, there is no permanent stream, but merely torrents which remain but a short time. As the ravine deepens, widens, and lengthens, thus approaching the underground water level and increasing the drainage area, the water remains for a longer and longer time after each rainfall. As the ravine conditions thus become more and more hydrophytic, the original flora, perhaps of shade mesophytes (as *Impatiens*), becomes replaced by amphibious shade plants, such

as the common buttercup (*Ranunculus septentrionalis*), *Plantago cordata*, various mosses, etc. Together with these forms algae of short vegetative period may be found in the wet seasons. When the ravine at last is sufficiently developed to have a permanent stream, a definite hydrophytic flora appears, consisting largely of algae (*e. g.*, *Batrachospermum*), aquatic mosses, and seed



FIG. 9.—Young island in the Illinois river at Starved rock (close view of island in foreground of *fig. 8*), seen from above, and showing the destructive action of the river.

plants with finely dissected leaves and strong holdfast roots (such as *Myriophyllum*), though these latter plants are more characteristic of ponds. In the early phases of a stream, the currents are rapid and the vegetation (apart from lower forms) is sparse, by reason of the difficulty which plants have in securing and retaining a foothold on the stream bed. This difficulty is due to the rapid erosion and consequent instability of the substratum, as well as to the direct destructive action of the currents. *Fig. 7* shows one of these young streams, whose flora is sparse.

Springs and spring brooks may be classed with ravine streams, but differ from them in the relative absence of erosion phenomena. This type of stream is uncommon in the Chicago area, though there are a few spring brooks near Chesterton. The water supply is much more constant than in ravine streams, and the shade of the ravines is often lacking. Besides the aquatics there may be mentioned a characteristic brookside flora, including such plants as *Symplocarpus foetidus*, *Asclepias incarnata*, *Chelone glabra*, *Poly-*

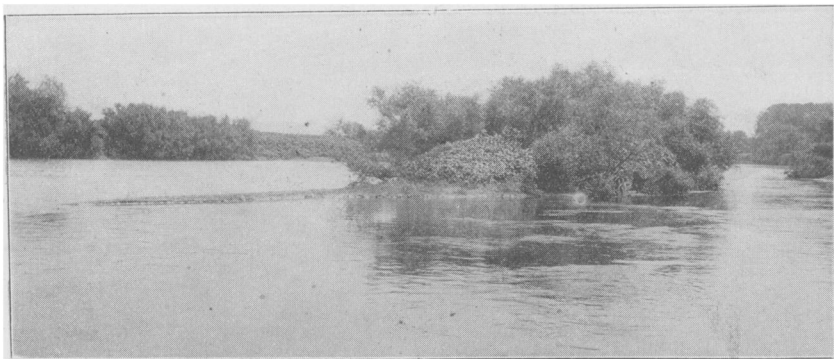


FIG. 10.—Same island as shown in *fig. 9*, but seen from below, and showing the constructive action of the river. Naked sand bar recently formed at the lower end of the island (left hand), *Ambrosia* farther toward the right, willows on the older part of the island (extreme right).

gonum sagittatum, and two or more species each of *Eupatorium*, *Lobelia*, *Mentha*, *Lycopus*, and *Bidens*. The most characteristic spring brook shrub is the alder (*Alnus incana*), though the extensive northern development of alder thickets has no parallel here.

As the energy of the developing stream is checked, the conditions for plant life become more favorable. In the quiet pond-like waters of an older stream there may be found many of the aquatics that frequent the ponds and lakes. In fact the flora that is given later as characteristic of half-drained ponds and lakes (such as Calumet lake) may be transferred almost bodily to sluggish streams, such as the Calumet and Desplaines rivers.

When streams are old enough and therefore slow enough to

support a pond vegetation, they have become essentially depositing rather than eroding streams, and we find there the development of a flood plain. While the river is still confined within narrow walls and may thus be called young, there may be embryonic patches of flood plain, representing alternations of erosion and deposition in the stream. *Fig. 7* shows such a con-



FIG. 11.—Flood plain of the Desplaines river at Glendon park, showing encroachment on the river. Willows in the foreground, cottonwoods farther back.

dition of affairs ; though the stream is young and more destructive than constructive at that point, there are to be seen small flood plain areas with their typical tree inhabitants.

There is no place where flood plain development can be better studied than on growing islands in relatively rapid and yet essentially depositing streams, such as the Illinois river at Starved rock. *Fig. 8* gives a general view of the Illinois islands and flood plain. In *figs. 9* and *10* the lower island (foreground of *fig. 8*) is seen close at hand. Any obstacle, such as a partially submerged tree trunk, serves to check the river current and cause a deposition of sand or silt, and before long a sand bar

originates. As in the case of a sand dune, the bar itself becomes an obstacle to the currents and hence continually grows larger. The first vegetation, as on the lake beach, consists largely of annuals, especially the giant ragweed (*Ambrosia trifida*); rushes and sedges, some annual and some not, are also present but are less conspicuous. The perennials that manage to survive one



FIG. 12.—Mesophytic flood plain forest in the bottoms of the Desplaines river at Riverside. Elms and basswoods. Rich herbaceous vegetation, consisting largely of Phlox.

season are largely washed away in the winter and spring, so that in reality the vegetation is almost exclusively annual. The first woody plants to get a more or less permanent foothold here are willows (*Salix nigra* and *S. longifolia*).

While islands of the above type gain more soil than they lose, a comparison of *figs.* 9 and 10 shows that the river erodes above and deposits below. As a consequence these islands migrate down the river, as well as grow in area year by year.

Hence the upper part of the island is the oldest, as the vegetation well shows. *Figs. 8 and 10* show at the lower end the sand bar, which comes to a point and is so young or so exposed to submergence as to be barren of vegetation. Next comes the Ambrosia, then the willows, and finally a characteristic flood plain



FIG. 13.—Flood plain forest along Fraction run at Lockport, showing a rather striking collection of southern trees (see text). Coffee tree in the foreground.

forest (background of *fig. 8*). The asymmetry of the river island vegetation is in striking contrast with the zonal symmetry of pond islands, as will be shown later (*fig. 19*). The cause is evident, viz., the relative lack of symmetry in river currents as compared with pond currents.

The gradual encroachment of the land upon a stream through continuous deposition is well shown along the Desplaines river, and to a less complete degree along the Chicago river and Thorn

creek. In the Desplaines bottoms the sand bar and island formations of the Illinois are largely absent, the currents being much less rapid. In the shallow water near the margin of the river are various hydrophytes, such as *Sagittaria*, *Rumex verticillatus*, etc. The outermost fringe of land at ordinary low water is often almost as barren of vegetation as are the islands, but the



FIG. 14.—Flood plain of the Calumet river near Chesterton, showing the beginnings of terrace formation, indicated more by the falling elm than by the topography.

soil is fine and hence makes a mud flat instead of a sand bar. Immediately after the spring freshets have gone, an alga vegetation is frequently found on these flats, consisting especially of *Botrydium* and *Vaucheria*. Later in the season annuals, or even scattered perennials, may occur here, though the winter and spring floods uproot or bury most of this vegetation. The *Ambrosia* and willow vegetation soon appear as described above. The river maple (*Acer dasycarpum*) usually appears with or soon after the willows. After the willows the cottonwood (*Populus monilifera*) and the ash (*Fraxinus Americana*) soon come in. Fig. 11 shows an advancing flood plain of this type; willows are seen on the margin and cottonwoods farther back.

Gradually the growing flood plain becomes dry enough to permit the germination and development of a true mesophytic flora. The trees named above, especially the willows, are largely replaced by others that seem better adapted to the changed conditions; among these are the elms (*Ulmus Americana* and *U. fulva*), the basswood (*Tilia Americana*), the walnut and



FIG. 15.—Terrace in the flood plain of the Desplaines river at Glendon park showing how a mesophytic flood plain may become xerophytic. The opposite bank shows deposition and flood plain enlargement (*fig. 11*).

butternut (*Juglans nigra* and *J. cinerea*), the pig-nut (*Carya porcina*). In this rich flood plain forest there are many lianas climbing over the trees, *e. g.*, greenbrier (*Smilax hispida*), grape (*Vitis* spp.), Virginia creeper (*Ampelopsis quinquefolia*), and poison ivy (*Rhus Toxicodendron*).

The undergrowth in these river woods is very dense and luxuriant, the alluvial character of the soil making it very fertile. Among the shrubs are the thorns (various species of *Crataegus*), the gooseberry (*Ribes Cynosbati*), and many others. The herbaceous vegetation is dominantly vernal, the shade being too dense for a typical estival flora. Prominent among the spring

flowering herbs are *Trillium recurvatum*, *Phlox divaricata*, *Polemonium reptans*, *Hydrophyllum Virginicum*, *Mertensia Virginica*, *Collinsia verna*, *Claytonia Virginica*, *Erythronium albidum*, *Arisaema triphyllum* and *A. Dracontium*, *Nepeta Glechoma*, *Isopyrum biternatum*, *Caulophyllum thalictroides*, *Viola cucullata*, *Galium Aparine*. Other characteristic herbs are the nettles (*Urtica gracilis*, *Laport-*



FIG. 16.—An oxbow lake in the flood plain of Thorn creek. The willows are subsequent, dating back to a stream margin, while the shrub (*Cephalanthus*) and herb vegetation is associated with the present undrained condition.

tea Canadensis), various umbellifers (*Heracleum*, *Cryptotaenia*, *Sanicula*, *Osmorrhiza*), and the parasitic dodder (*Cuscuta Gro-novii*). *Fig. 12* shows a characteristic mesophytic flood plain forest along the Desplaines river; underneath the elms and bass-woods is seen a rich herbaceous flora, consisting largely of *Phlox*, which the picture shows in full bloom.

In some of the bottom lands there is a rather striking collection of trees, whose chief range is mainly southward. *Fig. 13* shows a flood plain tree group near Lockport, most of whose members are largely southern, viz., the coffee tree (*Gymnocladus*

Canadensis), seen in the foreground, the papaw (*Asimina triloba*), the sycamore (*Platanus occidentalis*), and the hackberry (*Celtis occidentalis*). In other flood plains there may be found the mulberry (*Morus rubra*), the red bud (*Cercis Canadensis*), the buckeye (*Aesculus glabra*), and the tulip (*Liriodendron Tulipifera*). None of these trees are common in our district, and only *Celtis*



FIG. 17.—A dead oxbow lake in the flood plain of Thorn creek. A willow still remains at the right, while the shrubs (*Cephalanthus*) have closed in upon the lake.

may be regarded as frequent. These relatively southern trees are found not only along the Desplaines and its tributaries, where there is supplied a continuous habitat along the river southward, but also along the Calumet and its tributary, Thorn creek. The occurrence of the tulip tree is full of interest, since it has been found thus far chiefly (perhaps only) in the vicinity of the dunes. Its occurrence has been noted especially at Chester-ton along a small stream which empties into Lake Michigan at that point; the tulip tree has also been found away from present streams, but apparently in old valleys whose streams have been diverted by dune activity. The confinement of these southern

trees to flood plains is not strange, since in such habitats are given the most congenial conditions that can be found in our area.

The vegetation on flood plains is not always as described above. Sometimes meadows are found instead of forests; this condition is particularly well shown along Thorn creek. *Fig. 18* shows a stretch of meadow of this type. Besides various grasses



FIG. 18.—Flood plain of Thorn creek near Glenwood, showing a meadow instead of a forest. At the center is an uneroded island, detached from the morainic mainland, seen at the left. The vegetation of the island is similar to that of the morainic uplands.

(such as *Poa pratensis* and *Agrostis alba vulgaris*), there are often other plants in abundance, *e. g.* *Thalictrum purpurascens*, *Fragaria Virginiana*, *Anemone Pennsylvanica*. The ecological meaning of the meadow is not clear. Probably mowing or grazing is responsible for the failure of a mesophytic forest to develop. Extensive thorn (*Crataegus*) thickets sometimes occur in these meadows and probably betoken the beginning of a mesophytic forest. Extensive and apparently natural meadows are found in the Calumet valley.

As we have seen, the climax type of vegetation on the flood

plain is the mesophytic forest, but here, as well as on the river bluffs, the climax may be but temporary. Retrogression is almost sure to come in connection with terrace formation. While it is true that deposition is the main feature of flood plains, it is also true that erosion has not ceased; the downward cutting of the river once more causes vertical banks, though this time in its own flood plain. This action is seen in *fig. 14* which shows the beginning of the new erosive phase, and its indication in the falling elm. There has doubtless been lateral erosion here also, since elms are not usually marginal trees. *Fig. 15* shows the erosion of the flood plain still farther advanced; this bank is just opposite the willow vegetation shown in *fig. 11*, hence there is deposition on one side and cutting on the other. A river may thus swing quite across its flood plain, destroying all that it has built, including the mesophytic forest. Not only is the vegetation destroyed directly, as shown in *fig. 14*, but also indirectly, since the lowering of the river causes the banks to become more xerophytic. In place of the herbaceous mesophytes, *Equisetum* and other relatively xerophytic forms may appear, though the trees usually live until directly overthrown by the river.

One more phase of river activity may be briefly sketched. In meandering over a flood plain, serpentine curves or oxbows are frequently formed. In time the river breaks across the peninsula and the oxbow remains as a crescentic lake. The conditions radically change almost immediately, and the river life is replaced by pond life. The change is even more striking on the margins, where the old plants pass away and the forms of undrained swamps come in. *Fig. 16* shows the remnant of one of these oxbows; on the farther side are old and dying willows, trees that look back to the well drained river margin. On either side of the pond are seen clumps of the button bush (*Cephalanthus occidentalis*), one of the most characteristic plants of undrained swamps. Thus the willows are antecedent and the button bush subsequent to the formation of the cut-off. *Fig. 17* shows a portion of the same, in which the willows and even the pond itself have gone, and only the marginal button bush is left,

though in this case, the margin occupies the center of the original pond. Near Starved rock an extinct oxbow lake on the flood plain of the Illinois river contains an extensive patch of *Sphagnum* and *Osmunda*, among the most characteristic plants of undrained swamps. There are many undrained swamps, some with tamaracks, in the Calumet valley. The future of these swamps is like that of other swamps, and will be described in the next section. *Fig. 18* shows a morainic island in the Thorn creek flood plain; the stream has meandered but has thus far left this detached fragment of the morainic mainland with a large part of its original flora.

In closing the section on rivers, all that is needed is to emphasize again the idea that the life history of a river shows retrogression at many points, but that the progressions outnumber the retrogressions. Not only this, but retrogressive phases are relatively ephemeral. Thus a river system, viewed as a whole, is progressive, and through all its vicissitudes there is an ever increasing area of mesophytic forest. When the theoretical base level is reached there seems to be no apparent reason why mesophytic forests should not be developed throughout most of the great plain.

[*To be concluded.*]